darker markings on the costal margin close to the apex. The head, thorax, and abdomen pale greyish brown.

Expanse $4\frac{2}{10}$ inches.

*Hab.* Mexico, near Durango city (*Becker*).

A fine distinct species, allied to *P. argentiferus*, Walker.

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## XLIII.—*Observations on the Dentition of Mammals* *.

By W. Kükenthal †.

We do not yet possess a satisfactory explanation of the tooth-change of Mammals, as was shown by M. Schlosser‡ only a short time ago.

The conjecture that both series of teeth have been derived from the Reptiles is at once opposed by a number of statements, according to which in the lower orders of Mammals tooth-change is either entirely absent, or, as in the case of the Marsupials, is confined to one premolar. Flower's§ hypothesis, afterwards considerably expanded by Oldfield Thomas‖, that the milk-dentition represents a fresh acquisition on the part of the higher Mammals, and that the permanent series alone is the original one, could therefore be supported by many weighty reasons. From among the large number of views which differ from this in more or less material points, I will here merely allude to that of Baume¶, according to which both series of teeth have had merely a secondary origin. For Baume supposes that owing to the shortening of the jaws which set in in the course of the evolution of Mammals, the originally numerous and similar teeth could no longer find room in one series, so that a portion of them became displaced and were able to appear only later on, as the permanent dentition.

* I intend to give a detailed exposition of the present investigations in the second volume of my 'Vergleichend-anatomischen und entwickelungsgeschichtlichen Untersuchungen an Waltieren' (Denkschriften der mediz.-naturw. Gesellschaft in Jena, Bd. iii.).

† Translated from a separate impression from the 'Anatomischer Anzeiger,' vi. Jahrgang (1891), no. 13. pp. 364–370.

‡ M. Schlosser, "Die Milchbezahnung der Säugetiere," Biolog. Centrabl. 1890.

§ W. H. Flower, "On the development and succession of the Teeth in the Marsupialia," Phil. Trans., 1867.

‖ O. Thomas, "On the homologies and succession of the Teeth in the Dasyuridæ, with an attempt to trace the history of the evolution of the Mammalian Teeth in general," Phil. Trans. vol. 178, pp. 443–462.

¶ Baume, "Versuch einer Entwickelungsgeschichte des Gebisses": Leipzig, 1882.

Baume, like many other investigators, therefore regards as the original form a dentition consisting of numerous similar teeth, and consequently starts from the Edentates and especially the Toothed Whales as the primary type; I therefore commence by examining the latter.

Toothed Whales: The Toothed Whales are very generally considered as homodont; Weber*, however, is right in considering the tusk of the Narwhal and the lower canine of the Ziphioids to be vestiges of a former dissimilarity of dentition. In an embryo of *Phocæna communis* of nearly full time, I find a heterodont dentition tolerably sharply marked, since out of the twenty-five teeth in each half of the jaw, the posterior seven have two and sometimes three cusps.

If on the one hand it is open to doubt whether the Toothed Whales have an entirely homodont dentition, nevertheless on the other it has been regarded as an absolutely certain fact that the Toothed Whales are monophyodont, and that the single series of teeth which appears belongs to the permanent dentition. Weber, who adopts afresh an idea previously expressed by Julin†, is alone in suggesting the hypothesis ‡, that the dentition of the Toothed Whales comprises both series of teeth, which, owing to the enlargement of the jaws, were all able to appear at the same time.

My investigations in this direction so far embrace a considerable number of embryos of *Beluga leucas*, *Globiocephalus melas*, and *Tursiops tursio*; this is what I have discovered: The dentition of the Toothed Whales is a true milk-dentition, or, better, it belongs to the first dentition, which is permanent. Irrefragable proof of this is furnished by the appearance of rudiments of second teeth internally to those which persist; it is true that the former are considerably smaller and do not reach the surface, but they nevertheless possess a distinct crown of enamel, and even the characteristic enamel pulp.

In the Toothed Whales, therefore, the germs of both dentitions are found, and this cuts the ground from beneath those hypotheses which start from them as typical monophyodont animals; Weber's hypothesis, also, is no longer tenable.

Whalebone Whales: The Whalebone Whales, for which, since they have genetically nothing to do with the Toothed Whales, I claim a special order within the Mamma-

* Weber, 'Studien über Säugetiere': Jena, 1886, p. 196.

† Ch. Julin, "Recherches sur l'ossification du maxillaire inférieur, et sur la constitution du système dentaire chez le fœtus de la *Balænoptera rostrata*," Arch. de Biologie, 1880.

‡ Weber, *op. cit.* p. 134.

lian class *, have, as is well known, germs of teeth in the first third of their fœtal life; these are subsequently absorbed. Among recent investigators Julin † and Weber ‡ widened the difference which Eschricht § previously stated to exist between the nine anterior teeth and the posterior ones, by affirming that the latter are not simply conical but have several cusps, and that the dentition is absolutely heterodont.

My own investigations were carried out upon thirty different specimens of large jaws of fœtal Whalebone Whales, including *Megaptera boops*, *Balænoptera rostrata*, *Balænoptera Sibbaldii*, and *Balænoptera musculus*, which were partly preserved whole and partly divided into series of sections made in the three chief directions. In the first place I dispute such a difference as has been stated to exist between the nine anterior and the posterior teeth; the appearance of teeth which seem to have several cusps is, in my preparations of older jaws, occasioned by the process of absorption, which begins at the tip ‖. The posterior teeth are somewhat more convex than the anterior ones, but throughout are simply conical, with the exception of cases, which are of quite isolated occurrence, where a pair of neighbouring teeth are apparently fused together. The position of double teeth of this kind (three separate teeth or even four may also be united together) scarcely follows any definite rule; in a few cases they also occur among the first nine teeth, and even on this account they cannot correspond to the supposed molars, according to Julin's interpretation. Are these double teeth secondary fusions, or do they represent primitive conditions? Embryology furnishes the answer. A series of seven embryos of *Balænoptera musculus*, measuring from 43 to 82 cm. in length, shows that the number of the double teeth diminishes considerably with increasing growth, while the number of the separate tooth-tips in each half of the jaw remains constant at fifty-three. In the youngest stages nine or even fifteen teeth are fused together; in the following ones five, four, and three, and in the oldest only two. The same result, the diminution of the double teeth with increasing growth, is furnished by the comparison of younger and older embryos of other species of Whalebone Whales. It follows from this

* W. Kukenthal, "Ueber die Anpassung von Säugetieren an das Leben im Wasser," Zoologische Jahrbücher, 1890; Ann. and Mag. Nat. Hist. ser. 6, vol. vii. pp. 153–179.

† Julin, *loc. cit.*

‡ Weber, *loc. cit.*

§ Eschricht, 'Untersuchungen über die nordischen Waltiere': Leipzig, 1849.

‖ *Vide* also Pouchet et Chabry, "Sur l'évolution des dents des Balænides," Compt. Rend. Ac. Sc. Paris, tome 94, no. 8, pp. 540–542.

that the double teeth represent an original condition, and are therefore to be regarded as molars, and further that CONICAL TEETH, WITH SINGLE TIPS, ARISE FROM MOLARS BY DIVISION. We have thus learnt a method by which numerous homodont teeth arise from a small number of heterodont molars. I shall subsequently adduce the palæontological facts which substantiate such an origin of homodont from heterodont dentitions; I would here only further allude in all brevity to an analogous phenomenon which occurs in a Bearded Seal (*Phoca barbata*) from Spitzbergen.

Owing to mechanical causes (hard food, consisting of mussels, besides the final reason, which is the incomplete calcification of the teeth) the molars in the specimen before me have worn away, and, with the exception of the last, have each become more or less completely separated into two, which present an absolutely similar appearance; instead of five molars, we consequently find seven and eight unicuspid teeth.

The results of my embryological investigations decide the question whether the teeth of Whalebone Whales belong to the first or the second series, in so far as they show that rudiments of a second series of teeth are still present; the cord of epithelium in question is for the most part fused with the enamel-germ of the actual tooth, which therefore essentially corresponds to the first series. The teeth belonging thereto resemble in this the so-called true molars of all other mammals, which, as they have no precursors in the milk-dentition, are assigned to the second series, although they must be regarded as having arisen from the fusion of the rudiments of both dentitions. (In the case of the first molar this is often still distinctly demonstrable; it is to be seen with especial clearness in embryos of *Spermophilus leptodactylus*, for instance.)

I refer the peculiar transformations of the dentition in pelagic mammals, which have just been described, to mechanical causes, terminating with diminished calcification, which, as being necessary for the diminution of the specific gravity, is a phenomenon of very frequent occurrence in pelagic mammals, and, as has already been shown, also gave the first stimulus which led to the occurrence of hyperphalangy, as well as the loss of the dermal armature of the Toothed Whales*.

* In my paper on the "Adaptation of Mammals to Aquatic Life" (Zool. Jahrbücher, 1890 [Ann. and Mag. *loc. cit.*]), I explained these views in greater detail. Of the former presence of a dermal armature in Toothed Whales, which I inferred from grounds of comparative anatomy and embryology (Anat. Anzeiger, 1890, p. 237), I am now able to adduce palæontological proofs also.

Edentates: embryos of *Dasypus novemcinctus* exhibit the typical formation of successors for the first seven teeth; a successor is wanting only in the case of the last tooth. The occurrence of tooth-change in this animal has already been demonstrated by Tomes. Moreover in the lower jaw of the embryos I find not eight teeth, but eleven, of which the three first are smaller and do not cut the gum. I am now also able to mention a second Edentate which has rudiments of two dentitions: this is *Dasypus villosus*. This phenomenon consequently appears to be of very general occurrence among the armadilloes. Whether actual tooth-change really takes place is of no consequence for my purpose; I merely affirm the presence of rudiments of milk and second teeth.

Marsupials: Flower, who was afterwards followed by Thomas, bases his hypothesis that the milk-dentition is a secondary acquisition on the part of the higher mammals, on what takes place in Marsupials, in which either no tooth-change or only the change of a third premolar occurs. The dentition of Marsupials is very generally assigned to the second series, and the precursor of the third premolar regarded as a milk-tooth. My own investigations upon this group have so far extended only to the study of a series of young specimens of *Didelphys* of different sizes. On the basis of these investigations I assert that THE PERMANENT SET OF TEETH IS TO BE ASSIGNED TO THE MILK, OR FIRST DENTITION, and that only one second tooth, the subsequent third premolar, occurs. I can easily furnish the proof of this, as soon as it is granted, that the two dentitions are also distinguishable from the point of view of morphology, besides being so from the physiological standpoint of the difference in the time of their appearance. The rudiments of the two dentitions, which have a common origin in the primitive dental fold, are so disposed, that the first set of teeth is developed from the outer one, and the second from the inner. Now my preparations show that this is the case not only in the third premolar, but that the tooth-rudiments lying in front of it, especially those of the incisors, also possess on the inner side, branching off from the neck of the epithelial invagination, a distinct twig of epithelium with a knobbed end; and this must be regarded as the earliest rudiment of the enamel-organ of the second tooth. It at all events follows from this that the entire dentition of the opossums is to be ascribed to the first and not to the second series. The mainstay of the hypothesis of Flower and Thomas, that the milk-dentition has been secondarily acquired by the higher mammals, is thus destroyed.

The following conclusions result from the foregoing investigations into the dentitions of mammals. The rudiments of both dentitions occur not only in the higher mammals, but also in the lower orders of Marsupials, Edentates, Odontocetes, and Mystacocetes. THE EARLIEST MAMMALS WERE DIPHYODONT. The monophyodont and homodont condition of many mammals, *e. g.* the Toothed Whales, has been secondarily acquired. Within the mammalian class, ascending from the lowest to the highest forms, we see how the second dentition gains the upper hand more and more as regards form and function, while in the lower forms the first dentition is predominant. In the rudimentary stage both dentitions are of equal value; embryology gives us no support for the often-expressed assertion that one of the two dental rudiments has arisen in dependence upon the other; they are both sisters, whose mother is the simple invagination in the jaw, which we term the dental fold ('Zahnleiste').

Now can we discover a bridge which connects the dentition of Mammals with that of their ancestors, the Reptiles?

There are no absolute differences between the mammalian and reptilian tooth, as has already been shown by Seeley *; not one of the characters of the mammalian tooth is perfectly constant; the loss of any one of them is an approximation to the reptilian tooth, and conversely reptilian teeth often assumed characters belonging to those of mammals. The replacement of teeth moreover occurs in reptiles to a still greater extent than in mammals, since several series of teeth may follow one another, the rudiments of which, as in the case of the second dentition of mammals, are formed internally to the first. The idea of deriving the dentition of mammals from that of reptiles therefore does not appear to me to be too hazardous; of the several series of teeth which are found in reptiles, only two still persist in mammals.

In conclusion I would subjoin the following attempt to explain the origin of molar teeth in mammals, while freely admitting its purely hypothetical nature. Owing to our investigation of tooth-germs in Whalebone Whales, we have become acquainted with the phenomenon of the division of the molars in mammals, whose jaws become elongated, into a multitude of conically pointed structures, resembling the teeth of reptiles. Conversely, have not the molars of mammals also arisen in this way, in that, in consequence of the reverse process, a shortening of the jaws, which the ancestors of existing mammals underwent in the course of their trans-

* H. G. Seeley, "On the Nature and Limits of Reptilian Character in Mammalian Teeth," Proc. Roy. Soc. Lond. vol. xliv. pp. 129–141.

formation from reptile-like progenitors, a number of simple, conical reptile-teeth came together to form each mammalian molar? Palæontology is in favour of my view; the oldest known mammals, e. g. *Triconodon* from the Upper Jura, exhibit molars of the typical structure requisite for our idea, each consisting of three similar conical tooth-segments, lying one behind the other and fused together. The admirable papers of Cope, Osborn, Schlosser, and others have shown that from the triconodont, that is the tricuspid type, the molars of all mammals may be derived.

A multitude of questions as to the specialization of the teeth within the various orders, the teeth with continuous growth, the formation of roots, &c., still remain to be answered; I shall make the attempt to do this in a detailed account of my investigations.

Jena, June 5, 1891.

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## XLIV.—*The Dentition of* Didelphys: *a Contribution to the Embryology of the Dentition of Marsupials* *. By W. Kükenthal †.

In the case of *Didelphys* the dental formula $\frac{5}{4}\frac{1}{1}\frac{3}{3}\frac{4}{4}$ is very generally accepted. The tooth-change is limited to one tooth, the last premolar, as was first discovered by Gervais and Flower to be the case in Marsupials. By this discovery the older view that in Marsupials the whole of the teeth are replaced with the exception of the four molars was finally overthrown. The question, however, now arose as to how the dentition of Marsupials was to be regarded, *i. e.* whether it corresponds to the milk-dentition or to the permanent series of other Mammals. While Owen was rather inclined to adopt the former view, the latter was maintained by Flower,

* Translated from a separate impression from the 'Anatomischer Anzeiger,' vi. Jahrgang (1891), nos. 23 and 24, pp. 658–666.

† In a paper which was recently published in this periodical, entitled "Einige Bemerkungen über die Säugetierbezahnung" (Anat. Anz. 1891, p. 369 [*vide suprà*, "Observations on the Dentition of Mammals," pp. 279–285]), I have already alluded to the chief result of my investigations, which formed the subject of an address delivered on the 30th of May of the present year in the Aula of our University. But, in consequence of the delay which has arisen in the setting-up of my detailed statements owing to the compositors' strike, I am now induced to give herewith a somewhat closer proof of my assertions, at least as regards the Marsupials.